THE MEANING OF TREE-LIFE.

By Henry L. Clarke.[1]

(*Continued from Volume 28, page 472*).

It is a striking fact that the older fossil forest remains, at least through the Paleozoic and early Mesozoic strata, present a wonderful likeness in character the whole world over. The wide scattering and spreading of types that this indicates, is to be directly accounted for partly by the more frequent physical changes that took place in early geologic times, and the constant changes and shiftings in the relative positions of continental surfaces, through upheavals and subsidences; and in part by the wide wind-dispersion possible for the spores of the Paleozoic Cryptogams. Past question geology makes countless blunders in assigning strata in different parts of the world to the same age because of likeness in their fossil flora (and the statement holds almost equally true of fauna), where likeness is in fact a positive proof that the strata are not synchronous. But the chances for error in this direction decrease from the latest to the most remote ages. All evidences indicate more and more homogeneous climatic and physiographic conditions as we trace the geologic record farther and farther back.

When the low insular character of the early continents, and the consequent increased humidity of the atmosphere extended a nearly sub-tropical climate to the poles, it is obvious that the potency of the sun as a maker of the seasons and and zones, counted for far less than now,—unless indeed the sun itself were tremendously hotter then than now. But that this last supposition is false within the history of vegetation is proven by a simple fact. Were it true, the equatorial zone would have been a region of such intense heat that it would have formed an impassable barrier between the floras of the

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north and south polar regions; whereas, on the contrary, we find identical types to the far corners of both hemispheres.

It is a vitally important consideration that a slight increase in general atmospheric humidity would have the effect of converting the atmosphere into a heat-distributing oven.

We cannot indulge in the absurdity of asserting separate centers of identically similar development, and we know that the torrid zone of even the present would be impassable to perhaps 99 % of our far north temperate flora; so here is proof sufficient of relatively great homogeneity in the conditions of the far past, and increasing heterogeneity thence down to the present. Aside from the greater stability and ruggedness of modern continents, the change that has wrought an all important effect upon vegetation, has been the development of the modern widely extended continental land-areas, producing a secular diminution in the general humidity of the earth's atmosphere, with the consequent full development of the great climatic zones, the polar, temperate, and torrid. Probably in the later Mesozoic and early Tertiary, this change began to make its influence most strongly felt, and through the Tertiary down to the present its effect has steadily and rapidly become more and more obvious. The fact is of course not to be lost sight of, that the highly specialized Mesozoic and Tertiary floras would be far more susceptible than the more lowly Paleozoic to climatic changes. But the working of these changes has been all-powerful in making most of the problems of geographic botany that are before us in the present, and so we may here fittingly turn the course of our discussion in this direction.

The progressive changes from the comparative homogeneity of conditions in remote ages to the world-wide heterogeneity of the present, have been recorded in the development of more and more complex tension systems between the various factors of vegetation. Of these systems, the most primitive was that belonging to each individual forest,—a central stronghold of old established types, merging into a tensional margin line of newer, weaker forms. Wherever vegetation existed, this tension system must have existed; but while we see it in the

present world under an indefinite variety of aspects, probably in Paleozoic times a study of the tensions of one forest would have been, in the main, a study of all others. The far more homogeneous climatic and physiographic conditions then prevailing, must have meant almost as striking world-wide similarity between all forest tracts, as there is now bewildering diversity. New forms were far more rapidly dispersed from the localities where they originated, and wherever they migrated they found conditions practically similar and hence equally favorable. Thus within a comparatively brief range of time, closely similar floras might have been found in widely separated regions. But another factor came into play at an early period to greatly complicate the problem—the physiographic irregularities in continental surfaces. The increasing stability of physiographic features from remote toward modern times, has made these features vastly more complicated and diverse now than in ages past, and consequently their influence on vegetation has become more and more profound. The earliest, as well as all the subsequent manifestation of this influence, was the development of a second great system of tensions—tensions between the unlike vegetations of adjacent unlike country surfaces, between the swamp and the dryer plain, the flat country and the hills, the mountain sides and the valleys. Here the tensional margin lines of two diverse hosts of vegetation met and formed another tension line between their own, and on this, the struggle for the mastery waxed fiercest, and the evolution of highly specialized forms was most active.

Such were the two tension systems of preeminent importance in the early history of plant-life; later a third came upon the stage, brought into existence through the development of the great climatic zones. Probably this first began to assume decided importance, as has been pointed out, sometime in the later Mesozoic, and increased the range of its influence through the Cretaceous and Tertiary, till in modern times, it has culminated in producing the broadest and most fundamental division of the world into great botanical realms. That there were regions of glacial cold in Australia, India, and Cape Colony in Carboniferous times is an undoubted fact;

that there were regions of glacial cold in previous, as well as several subsequent, ages is highly probable; but this does not invalidate the general principle suggested here. The reconstructive meteorology of the near future will probably demonstrate that the geographical distribution of the Carboniferous glaciation, and of several other similar cases, is directly connected with peculiar stages of continental evolution and oceanic extension. And while such glaciations are of far-reaching importance for their age, they are nevertheless temporary "perturbations" that do not, in the long range of time, break down the secular increase in the direct subordinating of the zonal world-climate to astronomical, rather than terrestrial, influences. From a nearly homogeneous climatic condition throughout the world, there were gradually developed five fairly distinct zones merging into each other at their adjacent margins—a torrid equatorial, frigid polar, and temperate intermediate. Their development inevitably had a profound effect on vegetation. In the fossil forest beds of Cretaceous times in far northern regions, there have been found side by side Cycads, Conifers, Palms and Hardwood trees, a conglomeration utterly bewildering to the botanist of to-day, but nevertheless a typical indication of the relatively homogeneous climatic conditions of the age when such a forest could have existed.

With such a suggestion of the Mesozoic world before us, let us watch the great climatic zones develop. It is the tree-life of the forests that tells the story most clearly; to it belonged preeminently the all-important mission of remodeling the aspect of the world's vegetation. The trees moved their habitats, and the herbaceous forms were carried along with them. In the equatorial belt were all the conditions of heat and moisture most favorable to the vigorous development of plant life; in the polar regions that sternest foe, steadily increasing cold; in the temperate belts, a compromise between the conditions of the others. From the original mixed forest a selection had to be made of the tree-groups that were to hold dominion respectively over each of the new sets of conditions. How? It will not do to say glibly, the Palms

loved the heat, the Conifers the cold, and the Hardwood trees the happy medium. Conifers luxuriate to-day in the torrid zone, and Hardwood trees and modern congeners of the Palms once grew together in Greenland. No innate partiality for heat or cold separated the three great groups, but the stern laws of plant dynamics that determine the course of the struggle for existence. The old established and all-powerful tree-group, the patriarchs of the forest, were the Conifers, the group best fitted to stem the tide of change and battle with opposing conditions; next them in power, because most like them in character, were the Diclinae; and weakest were the Palms, the group whose foot hold was most precarious. These last could hold their own against the powerful Conifers and Diclinae only so long as climatic conditions were most favorable. Consequently, as the cold advanced from the polar regions the palms retreated toward the torrid zone. Here they took their stand, their highly specialized structure asserted its full power, and gradually they crowded out the Conifers and Diclinae, and established preeminent dominion over the equatorial belt. The Diclinae and Conifers were crowded out, "not that they loved heat less, but that they loved freedom more." They were fitted to maintain themselves against the cold of extratropical regions, and in these regions they were relieved from the struggle with a powerful competitor, the whole family of Palms and its associated rank luxuriance of tropical vegetation. In short, the strength of the Palms when congested into the equatorial belt, more than counterbalanced the loss sustained by the coniferous and hardwood trees in the cooling of extra-equatorial regions. And so the Palms, and with them the remnant of their ancient allies, the Tree-ferns and Cycads, claimed the tropics for their heritage. There was probably no region of the world where Conifers had not gained a strong foothold in the long course of ages; there is scarcely a corner of the modern plant-world that does not hold some group of them; and it was the Coniferæ that obstinately held their own against the cold of sub-polar lands, with the stubborn endurance that four great eras of geologic time have helped to build.

The Diclinae retreated before the advancing cold into more temperate climes, retreated in fact until they gathered strength to wage equal battle with their mighty coniferous opponents.

Here, in the temperate zones, the Diclinae stood fast and crowded the Conifers outward toward the polar regions, not toward the equatorial, for there the odds against the emigrants would be tenfold increased. The record of this battle of the trees is stamped upon many of the forest monarchs that we marvel at to-day. A recent writer has well said: "Just as in the formidable armor of some extinct armadillo one may read somewhat of its struggles with its enemies, so in the one hundred meters of solid trunk and in the massive girth of a living Sequoia gigantea, the giant red-wood, one may learn of its struggles in the ancient forests of Cretaceous and Tertiary times, when its allies and competitors were alike more numerous."

The third great tension system is now unfolded before us. We see the hardwood forests of temperate regions facing on the one hand the congested luxuriance of equatorial vegetation, and on the other the ancient coniferous forest gathered round the poles and step by step forced backward by advancing cold. There is a great equatorial pressure toward the poles, and an opposing polar pressure, traceable to opposite causes; and between them there is a broad tension line, the temperate zones. Conway MacMillan, who was quoted just above, has proposed a broadly generalized division of the world into two great botanical realms, the Central Realm and the Distal Realm. But the division should be carried a step farther; taking the three great forest elements as a guide, we may fully express the evolutionary history of plant dynamics by recognizing three great divisions:—

The Central Tropical Realm, the Tensional Temperate Realm, the Distal Sub-Polar Realm. The three merge into each other and their elements are everywhere somewhat commingled, but in the main they are fairly distinct. Such was the general plan of the plant world of the late Tertiary, proximate Preglacial times. The Glacial Period had a wonderfully interesting effect in modifying the northern

portion of it. The story has been often told, but one aspect of it will deserve further attention. Out of the various forests of north temperate regions, we may recognize four that are of peculiar interest. The European, the Northeast Asian, the Appalachian, and the Pacific North American. All are relics of the preglacial northern forest, but they are relics in very different stages of preservation. The Northeast Asian is a marvel to students of tree-life in the abundance and immense variety of its forms. Evidently it has best preserved the characters of the primaeval forest. The poverty of the European forest is equally striking and has been well explained by the fact that the east and west mountain chains and the Mediterranean to the south were fatal to the vegetation retreating before the advancing glaciers. The Atlantic North American, or Appalachian forest, on the contrary, was well preserved by the physical characters of the country, and in its perfection is second only to the Northeast Asian. But the Pacific North American is an anomaly. It is preeminently a forest of Conifers with an astonishing poverty of hardwood types, although the latter are abundant as fossils in the Tertiary strata of the region. But is this such an enigma as it has often been considered? The ice sheet that swept over the Great Lakes and down into the Mississippi Valley did not reach that Pacific forest region of the United States, but its influence was felt there none the less surely. Before it retreated—first the Hardwood forest, and close on its heels the Coniferae. The Coniferae invaded the strip along the western slope of the Rockies, and also the great Northeastern Asian forest region, and remained in both, about equally strong in number of species. But in the case of the first named region what became of the Hardwood forest that pushed ahead of the Conifers? Behind it on the east were the Rockies; before it on the west the Pacific; and to the south the stern physiographic obstacles of the Mexican coast. And again, what was the character of the coniferous forest that invaded the Pacific strip? We need only point to the two Sequoias, sempervirens and gigantea, the "Big Trees" of California, the culminating triumphs of vegetative energy in Coniferae. The

Pacific strip became the refuge and stronghold during glacial times of the mightiest phalanx in the North American coniferous forest, and there they have stayed, simply because all competitors perished before their invasion. Obviously the conditions in the case of the Asian coniferous invasion were vastly different; while the comparative poverty of the coniferous element in the Appalachian forest is directly traceable to the strength of its hardwood element and the path of retreat afforded the Conifers toward the north and northwest.

A remarkable example of the development of higher types along the tensional margin-line was the glossopteris flora of the Carboniferous glacial regions,—a flora an age ahead of that of the rest of the world, and developed where the latter flora was beaten back by the glacial cold.

Many details of great interest to the systematic botanist might be outlined in this connection, but what has been suggested suffices to show how vitally important is the chapter of plant-history recorded in the world's tree-life. It will be found on comparison, that the record of the development and migrations of shrubby and herbaceous plants closely accords with the history of the tree-groups with which they are most closely allied. But the stability of tree characters vastly exceeds that of the characters of the lesser plant forms, and hence it is these latter that vary most in passing from one region to another. Still in this latitude we may clearly observe that the more ancient herbaceous forms are the more northerly in their range, and the newer the more southerly. The equatorial belt has become the great center of developmental activity, and out from its congested tension-margins come the vanguard of our highest floral types. The coniferous trees were all-powerful in the Mesozoic; the Hardwood trees of the amentaceous and choripetalous Dicotyls seem to have reached a climax of luxuriance in the late Tertiary; and out of the great element of sympetalous Dicotyls that predominate the herbaceous flora of the present world, there may be developed another great tree group that shall rule the forest of the far off future. The promise of this last is already to be found in the arborescent Compositæ of certain of the Pacific

islands. But it is certain that forest development in the future will follow no such clearly defined courses as in the past; the wonderful complexity of the geographical botany of the present has forever sealed the possibility of another distinctive tree-group attaining such a world-wide prominence as either the Conifers or the Diclinae or the Palms. These three must stand alone as a unique monument to the struggle for existence in the primaeval Mesozoic forest. For even as the conditions of that age made possible a remarkably homogeneous plant world, even so the great tension system of the earth's present vegetation makes diversity, to an equally or more remarkable degree, the key-note of future development.